

Fractional Integrated Stomatal Opening to Control Water Stress in the Field

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ABSTRACT

The usefulness of totally automated irrigation control systems is well established. Mass-flow porometers can be used as the sensing and feedback elements to implement such a system for the experimental control of water stress in the field. This study was conducted to determine if consistent relationships could be established between the mass-flow readings and other water-related physiological parameters. A range of stress conditions were imposed on plots of corn (*Zea mays* L.) by the system during the 1986 and 1987 field seasons in Greeley, CO. Midday leaf xylem water potential, leaf diffusive conductance, and year-end grain yields were measured during both years. In 1987, additional measurements were made of the infrared canopy temperature for calculating the Crop Water Stress Index (CWSI), and individual kernel weights and numbers, to determine the components of the grain yield predictions observed in 1986. Reductions in the number of kernels produced per unit land area were associated with stress-induced delays of silking relative to pollen shed. Additional yield reductions in some treatments were attributable to reduced weight per kernel. Significant correlations were found between the mass-flow sensors and grain yield and CWSI. The relationship between grain yield and stomatal conductance was consistent over both years, suggesting that the cumulative mean conductance may be useful as a yield predictor.

THE DESIRABILITY of automatically controlling water-deficit stress in field situations has long been recognized from both scientific and production viewpoints. The principles for such a stress control system were first outlined and demonstrated by Fiscus et al. (4,5). In that work, mass-flow porometers, which sense stomatal opening based on the resistance to bulk flow of gas through a leaf, were used as the sensing and feedback elements in a totally automated irrigation control system. A brief history, as well as further relevant references are given in Fiscus et al. (4). The logic behind the use of stomatal sensors for such a purpose was that the stomata constitute the control point for transpirational flux. Any condition that interferes with water movement to the leaf, primarily low soil water availability, would be indicated by a diminished degree and/or duration of stomatal opening in response to sunlight. Also, since stomata influence the rate of CO₂ diffusion into the leaf, C fixation may also be affected, with a resultant reduction in dry matter production and yield.

Use of the mass-flow control system in the field resulted in substantial increases in water application efficiency, defined in terms of grain yield per unit water applied, as well as reducing by about one third the amount of water necessary to optimize yields (5).

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Other experiments (3) demonstrated that the mass-flow porometers can track stress-induced changes in both leaf xylem pressure potential (ψ_{lx}) and leaf diffusive conductance (g_l). Relationships between these three measures of stress, however, were variable over repeated soil drying cycles. The value of ψ_{lx} at which stomata began to close was especially troublesome, due to the well-known conditioning of this relationship by previous stresses. In any case, the data suggested that the mass-flow measurements might be more sensitive to the onset of stress than g_l and especially ψ_{lx} , particularly after the first stress cycle. Furthermore, in extensive work with wheat and soybean, Oosterhuis and Walker (13) clearly demonstrated the reliability and usefulness of g_l as an indicator of the onset and development of stress and concluded that it is indeed a more sensitive indicator of stress than ψ_{lx} and more stable in a fluctuating environment than canopy temperature measurements.

Because our previous work did not include detailed concurrent physiological measurements, this study was undertaken to clarify the relationships between crop yield, mass-flow measurements, and the more conventional measures of stress such as g_l , ψ_{lx} , and the Crop Water Stress Index. Further, we will demonstrate that control systems based on mass-flow porometry are not only workable, but that they can be used to determine basic water-related physiological relationships in the field.

MATERIALS AND METHODS

Corn (*Zea mays* L. cv. Garst 3732, at a plant density of 72 000 plant ha⁻¹) was grown during the 1986 and 1987 seasons at the Northern Colorado Demonstration Research Center near Greeley, CO, on a Nunn clay loam soil (fine, montmorillonitic, mesic Aridic Argiustoll). The fields were fertilized with 112 kg ha⁻¹ N prior to planting in both years and an additional 84 kg ha⁻¹ N in 1986 during cultivation. Inadequate soil moisture conditions in spring necessitated early deployment of irrigation lines and prevented application of the additional N in 1987.

In both years, a nonreplicated experimental design consisting of four controlled irrigation treatments was used. The irrigation control-point designations, called trigger levels and ranging between 0 and 1, indicated the degree and duration of stomatal opening relative to the well-watered state. While three of the plots were subjected to continuous irrigation control, the fourth was allowed to cycle between periods of adequate soil moisture and severe stress. The irrigation trigger point in the latter plot, called the cycle plot, was initially held at 0.9 for several days to ensure well-watered conditions for the crop. The trigger was then reset to 0.0 until severe stress symptoms developed. Severe stress was characterized by visible stunting of growth compared with the well-watered plots, leaf curl, visible changes in leaf color, and stomatal opening at or very near zero relative to the well-watered plots. When such symptoms were ob-

Abbreviations: CWSI, Crop Water Stress Index; FISO, fractional integrated stomatal opening; IPI, integrated photosynthetic irradiance; ISO, integrated stomatal opening; MST, Mountain Standard Time; PPFD, photosynthetic photon flux density; PVC, polyvinyl chloride.

served, the trigger was reset to 0.9 for several days to allow recovery. After recovery, the process was repeated as many times as the length of the season allowed. The actual duration of the soil drying periods varied depending on the growth stage, precipitation events, atmospheric demand, and the water-holding capacity of the soil.

The trigger point of one of the other three plots, referred to as the control, was set at 0.9 for the entire season. Another of the plots, the sustained-stress plot, was set at 0.5 for the season, and the last plot, called the early-stress plot, was initially set at 0.5 until prior to tasseling and then raised to 0.9 for the duration of the season. A variety of trigger points in these experiments was selected to establish a range of stress situations and to demonstrate not only that control is possible but also that the stress level can be altered at any time.

The four plots, with north-south rows, were 15 m (20 rows) wide and 23 m long with an additional 10-m buffer on the west and a 20-m buffer on the east. The experimental plots and buffer plots were trickle irrigated, with an emitter line devoted to each row and running the length of the plots. Emitters were placed at 60-cm intervals along each line, giving a 60 by 76 cm water-application grid.

Mass-flow porometer clamps, used to connect a low-pressure air supply to the abaxial leaf surface (Fig. 1, 2), were the same as previously described (3,4,5). As in the previous work, clamps were attached to the first fully expanded leaf from the top of the plant. Since we were interested in the stomatal response to light, it was necessary to move the clamps about twice per week during vegetative growth to keep them near the top of the canopy and well exposed to the sun. After tasseling, the clamps were routinely placed on the fourth leaf from the top and changed once per week. Attachment of the clamps for a period of ≈ 2 d resulted in

a circular area of discoloration on the leaf ≈ 2.5 cm in diameter (the size of the rubber cushion). At the center of the circle, however, the tissue at the entry and exit for air flow remained a normal green color. We were unable to detect any progressive changes in stomatal response when the clamps remained in place for periods of > 1 wk, so the discoloration did not appear to affect the water supply to, or normal functioning of, that leaf area.

The experimental system (Fig. 1) contains several modifications of the previous design. The source of gas was commercial compressed air, and the pressure in the main line was controlled by a Granville-Phillips¹ (Boulder, CO) Series 216 Pressure Flow Controller and servo-valve using a pressure transducer (Setra Systems, Acton, MA, Model 216-1) to provide the sensing and feedback signal. The pressure transducer, with a full scale range of 0 to 12.7 cm H₂O, was the same model as those used for the porometer pressure sensors. The line pressure was set and maintained at a nominal head of 7 cm H₂O. Air flowed to the center of the field through a buried 2.54-cm PVC pipe. From there it was distributed to the experimental plots via 1.59-cm polyethylene tubing, which was further reduced to 0.63-cm tubing at the site of the porometer. The air then moved through a 6.35-cm length of glass capillary tube (Fig. 1, 2), providing a fixed conductance in series with the plant leaf. The capillary tube replaced the fine-metering valves used in our previous work (3,4,5), at a considerable savings in cost and maintenance and an increase in precision. Conductance of the capillaries

¹ Mention of a product or company does not imply any endorsement by the USDA.

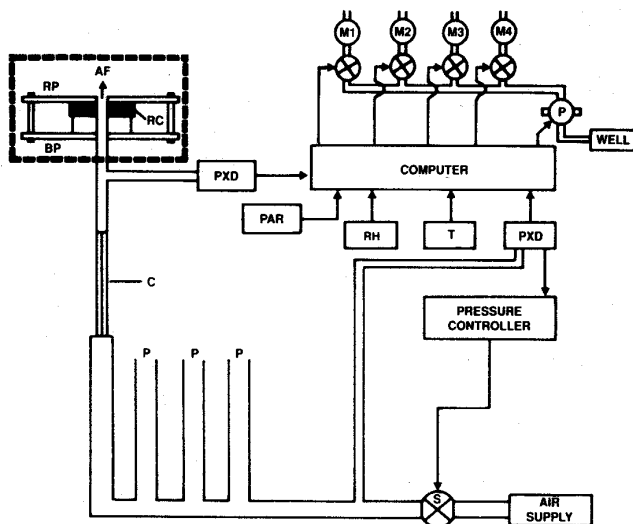


Fig. 1. Principal components of the mass-flow porometer sensors and irrigation control system. Only one porometer is shown but all were manifolded from the main air line. C = capillary tube; PXD = pressure transducer; S = control servo valve; T = air temperature; RH = relative humidity; PPFD = photosynthetic photon flux density from the PAR (photosynthetically active radiation) sensor; AF = air flow; RP = clear plastic retaining plate; BP = aluminum base plate; RC = rubber cushion; P (attached to the well) = water pump; P (all other) = porometers manifolded to the main air line. The solenoid-operated control valves directing water to the plots are attached to water meters numbered M1 to M4. Area enclosed by the dashed line is shown in detail in Fig. 2.

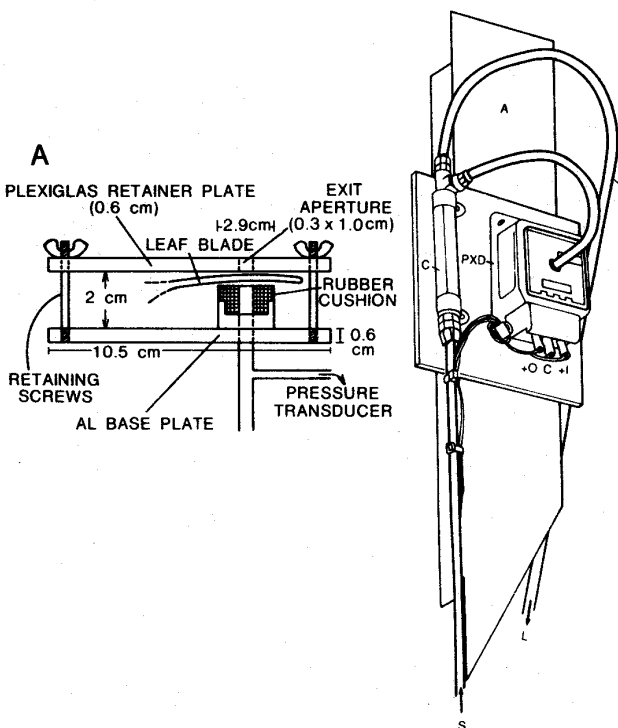


Fig. 2. Details of the porometer clamp, with a cross-sectional view with the leaf blade in position, and the capillary and pressure transducer field mounting. In the case of the latter: A = aluminum angle, driven into ground for support; C = capillary tube; PXD = pressure transducer; L = air line to leaf; S = air supply line; I+ = transducer excitation voltage; O+ = transducer signal voltage; C = common wire. The entire capillary-PXD assembly is covered with a plastic bag during field use.

was measured in the laboratory by monitoring the rate of air flow through the capillaries under pressures from 12.7 to ≈ 2 cm H₂O. The rates were linear with pressure across the entire range, indicating a constant conductance that averaged 1.008×10^{-3} cm³ s⁻¹ cm⁻¹ head ($\pm 0.060 \times 10^{-3}$ SD for a population of 20 capillaries and a SD for individuals of $<0.02 \times 10^{-3}$).

Finally, having passed through the capillary, the air reached the abaxial side of the leaf where it stopped and the pressure built up until it equaled the line pressure if the stomata were tightly closed. The degree of pressure build-up depended on the extent that stomata were open. If the leaf g_i was very high, then the pressure between the capillary and the abaxial surface fell to nearly zero.

For field installations, each pressure transducer and capillary tube pair was mounted on a 10-cm-square Lexan plate (Fig. 2), which was screwed to a 1-m length of 5-cm aluminum angle driven into the ground. The whole assembly was covered with a white plastic bag and tied at the bottom to secure it from the weather and small animals.

In addition to the measurements of porometer pressures in the plots, relative humidity (HMP 14U, Vaisala, Woburn, MA) and air temperatures (thermocouple) were measured with shielded instruments, along with PPFD (LI-190S Quantum Sensor, LI-COR, Lincoln, NE), in a clear area next to the plots. Each measurement, consisting of an eight-point average, was made once per minute, commencing at 0200 h (MST) every day and running until midnight. Every 10 min, the readings from each channel were averaged and stored in a disk file. Thus, 132 average values per day of PPFD, relative humidity, air temperature, and the pressure in each porometer were stored.

The measurement sequence was halted daily at midnight and the data collected during the previous 24 h were processed. Processing consisted of first integrating the PPFD measurements for the day to obtain an integrated photosynthetic irradiance. The integration was carried out by summing the areas under the curve for each 10-min interval throughout the day. Calculation of the IPI was followed by integrations of the duration and extent of stomatal opening based on porometer pressure readings. The latter procedure, which gave a value for the integrated stomatal opening for each porometer, consisted of first establishing a baseline pressure from the readings between 0200 and 0500 h. The readings for that day were normalized to the baseline, thus

converting the range of pressures to relative values between 0 and 1, with 1 representing the baseline pressure or fully closed condition. The resultant curve described the relative stomatal closure for that day. For convenience, all the values were then subtracted from 1 to convert them to values of relative stomatal opening, and multiplied by 100 to give a range of relative opening from 0% for full closure to 100% for full opening. The areas under the relative stomatal opening curve for each 10-min interval were then summed across the daily cycle to obtain the ISO in units of %h (percent-hours; e.g., 500 %h is the equivalent of a 50% stomatal opening over a period of 10 h). Previous work (3,4,5) showed that the ISO data, as a function of IPI, could be described as contained within a bounded area. The boundary line for that area was hyperbolic and represented the maximum possible ISO for any value of IPI. Thus we can write

$$\text{ISO}_{\max} = \text{IPI} / [k(\text{IPI}) + m] \quad [1]$$

where the coefficients k and m determine the maximum value and apparent shape of the line, respectively. An estimate of these coefficients was obtained by the following double reciprocal method, which is merely a rearrangement of Eq. [1]: First, $1/\text{ISO}$ was plotted as a function of $1/\text{IPI}$, and then a straight line was drawn between two data points such that all other data had ordinate values greater than or equal to the line (Fig. 3). The equation for this line is

$$1/\text{ISO}_{\max} = k + m(1/\text{IPI}) \quad [2]$$

where k and m are the intercept and slope, respectively, of the line in Fig. 3. Inserting these coefficients into Eq. [1] results in the boundary line shown in Fig. 4. Consideration of Eq. [2] also shows that $1/k$ is the asymptotic value of ISO that is approached as IPI approaches infinity. Thus, $1/k$ defines the upper limit of the ISO curve, while m is primarily a shape factor related to the rate of change of slope across the range of interest. It is also clear from Eq. [1] that the ISO_{\max} curve passes through the origin.

Figure 4 shows the boundary line for 1987 data calculated after completion of the season. Since the boundary line varied from year to year, it was necessary, in practice, to start the season with a previously determined average boundary line and then to update that line, if necessary, with data obtained early in the season.

The actual measured ISO for a day was divided by the ISO_{\max} value associated with the measured IPI for that day

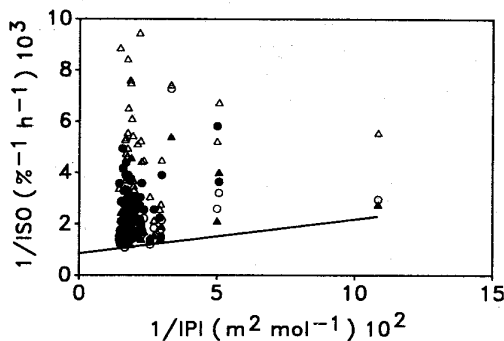


Fig. 3. Double-reciprocal method for determining the maximum integrated stomatal opening (ISO_{\max}) boundary line for 1987. The equation for the line is $1/\text{ISO}_{\max} = m(1/\text{IPI}) + k$ and defines the condition where all the data points are on or above the line. To reduce clutter and expand the scale near the region of interest, values of $1/\text{ISO} > 0.01$ have been omitted. Open circles = control plot; closed circles = sustained-stress plot; open triangles = cycle plot; closed triangles = early-stress plot. Each point is the average from four porometers. Values of k and m are given in Table 1 (1987).

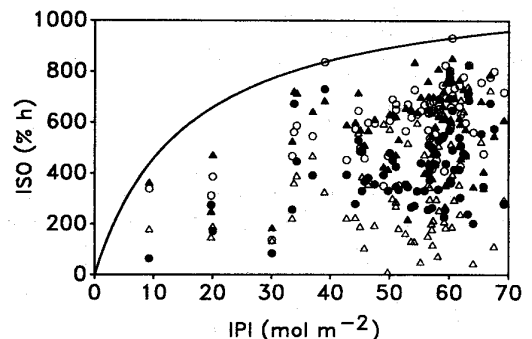


Fig. 4. Maximum integrated stomatal opening (ISO_{\max}) boundary line (Eq. [1]) and data for the 1987 season. The computer-drawn line represents the maximum possible ISO for any value of integrated photosynthetic irradiance (IPI) during the 1987 season. Open circles = control plot; closed circles = sustained-stress plot; open triangles = cycle plot; closed triangles = early-stress plot. Each point is the average from four porometers. Coefficients for this line were determined by the double-reciprocal method illustrated in Fig. 3 and are labeled in Table 1 as 1987.

to arrive at the fractional integrated stomatal opening. Each plot was fitted with four porometers, so the four FISO values for each plot were averaged and used as the control parameter for the automatic irrigation system. The on-line computer compared the average FISO for each plot with a preprogrammed trigger value chosen to establish the desired stress level. If the average measured FISO fell below the trigger value, the computer activated the appropriate solenoid valves and the pump to initiate irrigation in the selected plots.

The duration of the irrigation was calculated by a simple empirically derived proportioning algorithm designed to apply a minimum of 8 mm of water if the FISO was below the trigger, with an additional 0.2 mm for every percentage point that the FISO fell below the trigger. Thus, the amount of water applied was increased in proportion to the gap between the trigger and the measured FISO, whereas in previous work (3,5) the same quantity of water was applied regardless of how far the FISO was below the trigger. Water meters, which were installed in the main irrigation lines feeding each plot, were read daily as a check on the system.

Throughout the season, with an average frequency of about three times per week in 1986 (42 d total) and about four times per week in 1987 (63 d total), measurements were made of leaf xylem pressure potentials (ψ_{lx}) and adaxial and abaxial stomatal conductances (g_s). All of these measurements were made within an hour of solar noon, with the measurement sequence rotating among ψ_{lx} , g_s , and plot to minimize any temporal anomalies. Leaf xylem pressure potentials were measured with a pressure chamber (Soil Moisture Equipment Corp., Santa Barbara, CA) on the youngest fully expanded leaf from three randomly chosen plants per plot. When the plants reached their maximum vegetative growth, measurements were made on the fourth leaf from the top. For sampling, each leaf was covered with a plastic bag containing a moistened paper towel, severed with a razor blade at approximately one-third to one-half the distance from the base, and placed immediately in the pressure chamber. The pressure potentials were averaged for each plot.

Stomatal conductances were measured with an LI-1600 Steady State Porometer (LI-COR, Lincoln, NE) on leaves of the same age as those chosen for water potential measurements. Both the abaxial and adaxial surfaces were measured on three separate plants in each plot. The measurements from each surface for each plot were averaged, and then a total g_s for both surfaces was calculated, assuming that the two surfaces operated in parallel.

During the 1987 season, measurements of the infrared canopy temperature (Model 110 IR Thermometer, Everest Interscience, Woburn, MA) were also made about twice weekly, for a total of 26 d, during the same period as the ψ_{lx} and g_s measurements. Vapor pressure deficit was calculated from the relative humidity and temperature data acquired at the time of the infrared readings, and the Crop Water Stress Index of Idso et al. (8) was calculated following the protocol of Shanahan and Nielsen (17). The dates of pollen shed and silk emergence were measured for both years of the study by recording the percentage of plants in a center row of each plot that were shedding pollen and/or showing silk. The dates of pollen shed and silking were taken as the date when 50% of the plants were dropping pollen or silking, respectively.

Grain yields were measured on 25 plants per plot to provide estimates of plot yield. The procedure consisted of selecting five adjacent rows near the center of each plot to assure a uniform stand and to avoid the row ends. Plant population was established by counting the plants in the five-row stand. Then, ears from five alternate plants from each row were harvested, giving a pooled sample of 25 ears per plot. The ears were dried to a stable weight at 70 °C. The grain was separated from the cob and weighed. The

Table 1. Boundary line coefficients for 1986 and 1987. The first two sets of coefficients (1986i and 1987i) describe the boundary line used for irrigation control throughout the season while the other two sets were determined after the end of each season. The k and m are the intercept and slope of the double reciprocal plots (Fig. 3), and $1/k$ is the asymptotic value of integrated stomatal opening (ISO) as integrated photosynthetic irradiance (IPI) approaches infinity (Fig. 4).

Year	Intercept $k \times 10^4$	$1/k$	Slope $m \times 10^2$
	(%h) ⁻¹	%h	mol m ⁻² (%h) ⁻¹
1986i	8.62	1160	1.88
1987i	8.62	1160	2.50
1986	8.05	1243	0.56
1987	8.53	1173	1.33

weight figures were adjusted to 155 g kg⁻¹ moisture and corrected for the population density to calculate the grain yields in Mg ha⁻¹. In 1987, oven-dry weights of individual kernels (average of 1000 kernels) and numbers of kernels per unit soil surface area also were determined.

Relationships among mean seasonal values of the water-relations parameters were analyzed by least squares regression.

RESULTS AND DISCUSSION

Similar boundary lines were used to calculate ISO_{max} for purposes of irrigation control during both the 1986 and 1987 seasons according to Eq. [1] and the coefficients in Table 1. These coefficients are shown along with the coefficients for the actual boundary lines determined by the whole data set after the end of each field season.

The actual upper limit of ISO was ≈6% higher in 1986 than in 1987, and curves had higher maxima than the one used in the field for irrigation control (Table 1). The greatest discrepancy between the actual value and that used was ≈7%. In practice, a discrepancy of this magnitude makes little difference in the operation of the irrigation control system, since the trigger points are chosen simply to provide a desirable spread of nominal stress levels. Care must be taken, however, not to choose a trigger value too close to 1, since it may not be possible to maintain the system so close to the ideal. The control system depends on physical measurements that are subject to error. Making as many measurements as we did tends to minimize the effects of these errors, but any accidental overapplication of water in such a tightly balanced system might lead to soil saturation and root anaerobiosis. A likely result of such flooding would be to decrease root conductance, leading to partial stomatal closure the following day. Such a reduction in the FISO would compel the system to call for more irrigation, thus worsening the situation and leading to runaway irrigation demand. The eventual result probably would be substantial loss of crop yield. In practice, we found that a maximum trigger point of 0.9 is easy to maintain while avoiding the risks of overapplication.

The FISO values calculated during the 1987 field season and used for irrigation control are shown in Fig. 5A to 5D. The horizontal lines in Fig. 5A to 5C are the average FISO values over the part of the growing season that was under computer control. The split in the straight line in Fig. 5D indicates the change in the irrigation trigger point prior to tasseling. These

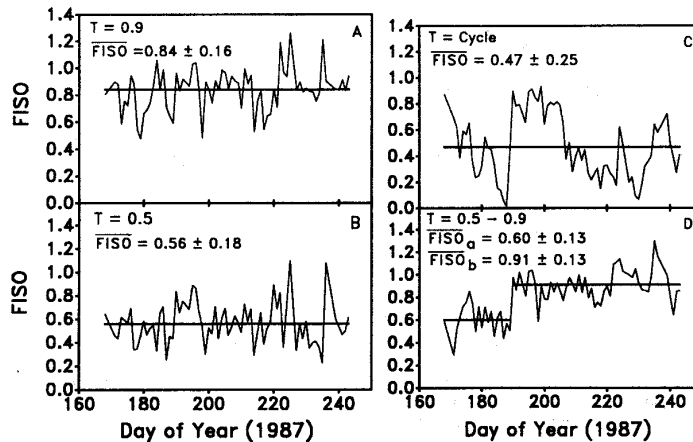


Fig. 5. Fractional integrated stomatal openings ($FISO = ISO/ISO_{max}$) for the four plots of 1987. T = trigger point for the irrigation control system. Mean FISO values, also appearing as the horizontal lines, and standard deviations for the season are given on the figures. The means for the separate segments of Fig. D are given separately.

mean values, especially in Fig. 5D, illustrate that it is possible to impose and maintain a range of stress levels, as indicated by FISO, in the field. Thus, not only can different levels of stress be imposed and maintained, but also changes in these levels can be arbitrarily initiated at any time. The rapidity of response of the system to desired changes depends on a variety of factors. Among these are the desired direction of change, natural precipitation events, water-holding capacity of the soil, and the soil moisture content at the time a change is initiated. Clearly, the system can respond more quickly to increases in the trigger level than to decreases, since water can be applied much more rapidly than it can be removed. A decrease from a high FISO (0.9) will potentially take longer than a decrease from an intermediate value (0.5), because the water supply for the intermediate value is already much more finely balanced against demand. Substantial natural precipitation events will, of course, make it very difficult to lower the FISO. The same is true for any amount of moisture in the soil profile in excess of daily demand. Rain exclusion shelters would alleviate most of these problems in controlling FISO and allow substantial improvements in the water application algorithms, thus reducing the day-to-day excursions about the control point.

It should be noted that Fig. 5 has a number of FISO values > 1 , a situation that should not be possible, but Table 1 provides an explanation. As stated earlier, a boundary line based on work prior to 1986 was used for the actual control of irrigation in both 1986 and 1987. Because this boundary line has a maximum ISO lower than indicated by actual field measurements, calculation of FISO from this boundary resulted in values > 1 . This is not a problem, however, since the trigger points may be reset at any time and the FISOs can be recalculated at the end of the season for reporting purposes. In the remainder of the data reported in this paper, however, we give the field-calculated values of FISO that were actually used for irrigation control (Fig. 5A to 5D). Also, the average FISO values reported are those shown in Fig. 5, with

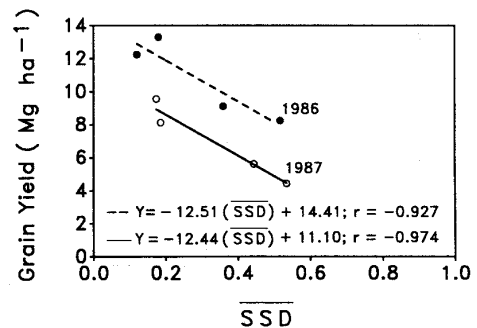


Fig. 6. Grain yield at 155 g kg⁻¹ moisture as affected by mean stomatal stress day (SSD).

the exception that the season-long average is used instead of the two segment averages from Fig. 5D.

A good linear correlation occurred between the grain yields and the average daily FISO over the season for both years of this study (data not shown). However, a more intuitive relationship may be obtained by using the average Stomatal Stress Day (SSD), which is defined as $1 - FISO$ (3). The decline in grain yield in proportion to the average SSD measured over the season is shown in Fig. 6. Assuming that the linear model is acceptable near the ordinate, the intercepts of these lines indicate the maximum possible yield for each season. The nearly parallel relationship of the lines indicates that each SSD decreased the yield by the same amount regardless of the maximum yield. The reason the intercepts are different for the two years is not known, but it is likely that they were determined by the reduced N fertilizer application in 1987 (only 57% of the 1986 rate).

Variation of the water-relations measurements across the imposed irrigation control treatments and their relationships to each other are shown in Fig. 7 to 9. The correlations between grain yield and mean g_s are quite good during both years of the study, with the highest yields in each year associated with the control plots and the plots that were held at an 0.5 control

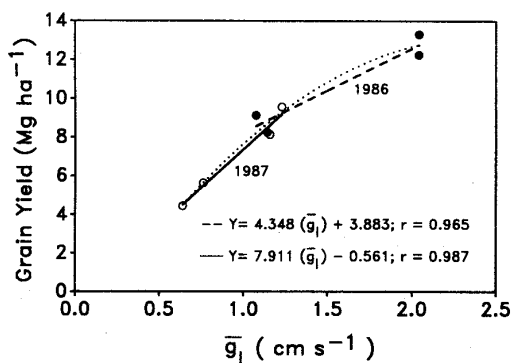


Fig. 7. Relationship between grain yield and mean leaf conductance (g_l) calculated over the season. The dotted curve is a second-degree polynomial fitted to both sets of data (1986 and 1987 combined) with the coefficients $a_0 = -2.8470$, $a_1 = 13.2161$, and $a_2 = -2.7256$; $r = 0.976$.

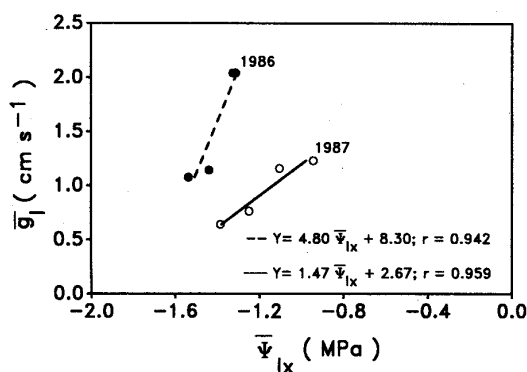


Fig. 8. Mean leaf conductance (g_l) as a function of mean leaf xylem pressure potential (ψ_{lx}). Intercepts on the abscissa are -1.73 MPa and -1.81 MPa for 1986 and 1987, respectively.

point prior to tasseling and then raised to control levels (early stress plots). In each year, the lowest yields were obtained in the 0.5 (sustained stress) plots and the cycle plots. In addition to the correlations being good for each year taken separately, a low-order polynomial fitted to the data from both years collectively still provided a good correlation. If the relationship in Fig. 7 can be shown to be reproducible, it could prove useful as a yield predictor. By averaging the daily leaf g_l values on a day-to-day basis as the data are obtained, it might be possible to predict the eventual yield of the crop at any time during the season. In the case where the cumulative average g_l predicts an unacceptable yield, the grower could take whatever action is necessary to improve the situation, if enough of the growing period remains to make that option worthwhile.

The relationship between g_l and leaf water potential (Fig. 8) was decidedly different during 1986 and 1987. Even though g_l was generally higher in 1986, the sensitivity to water potential as indicated by the slope was about three times as high as in 1987. Also, in 1986, the g_l values occurred over a lower and more narrow range of water potentials than in 1987. These data are consistent with numerous studies of leaf water relations as affected by N nutrition in wheat,

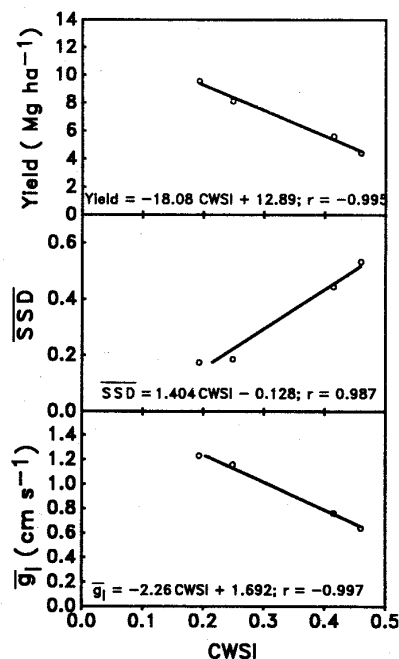


Fig. 9. Relationships between the Crop Water Stress Index (CWSI) and grain yield, mean stomatal stress days (SSD), and mean stomatal conductance (g_l) for 1987.

Triticum aestivum L. (11); rice, *Oryza sativa* L. (9,10); corn (1); cotton, *Gossypium* spp. (14–16); potato *Solanum tuberosum* L. (12), and *Amaranthus* spp. (7). The relevant results of these studies can be summarized as showing positive correlations between N nutrition and g_l . More specifically, N-deficient plants initiated stomatal closure at higher water potentials and the water potential threshold for stomatal closure was moved to lower values by increased N nutrition. Morgan (11) also showed that high-N wheat plants exhibited greater sensitivity to lowered leaf water potential during stress, an observation that he attributed to a greater susceptibility of the mesophyll photosynthetic capacity to water potential reductions. Since we made no gas exchange measurements during these studies, it is not prudent to pursue this particular point further. Even though we have no tissue-N measurements, it is quite reasonable to expect that since the 1987 N application was only 57% of the 1986 rate, N was the major contributing factor to yield and other physiological differences during the 2 yr of the study.

Analysis of the components of g_l reveals that if N nutrition were the primary yield-limiting factor in 1987, it had only a marginal influence on the mean ratio of abaxial to adaxial stomatal conductances. In 1986 this ratio was 1.08, compared with 1.00 in 1987, indicating a slightly lower abaxial conductance under N-limiting conditions. Because the mass-flow porometer cannot tell which leaf surface is limiting flow, it remains to be established whether the system will work well with dicots. In dicots the stomatal distribution between abaxial and adaxial surfaces is much more uneven and we might expect to see conductance ratios in the range of 1.5 or more under well-watered conditions.

Table 2. Linear regression coefficients for relationships not shown in figures.

Year	X	Y	Slope	Intercept	r
1987	CWSI†	LWP‡	1.438 MPa	0.696	0.971
1986	FISO§	g‡	2.708 cm s ⁻¹	-0.337	0.904
1987	FISO	g‡	1.589 cm s ⁻¹	-0.110	0.997
1986	FISO	LWP	-0.418 MPa	16.98	-0.712
1987	FISO	LWP	-0.980 MPa	18.22	-0.942

† Crop water stress index

‡ Leaf xylem pressure potential

§ Fractional integrated stomatal opening

¶ Leaf diffusive conductance

Table 3. Causes of total corn grain yield reduction for 1987. Fractional days for silking delays were calculated by interpolation. Kernel dry weights and numbers and given only for the control plot; all other plots are expressed as a fraction of the control value. Silking delay is relative to the control plot and the percent silking column is the percentage of plants in the sample which were silking on the first day when 100% of the plants in that plot were shedding pollen.

Control setting	Silking delay	Silking	Kernel weight	Kernels	Yield
FISO†	d	%	mg	no. m ⁻²	g m ⁻²
0.9	0	100	261	3216	839
0.5-0.9	1.5	81	0.85	1.06	0.893
0.5	2.5	44	0.96	0.64	0.613
Cycle	2.0	60	0.65	0.88	0.571

† Fractional integrated stomatal opening

The intercepts on the abscissa of Fig. 8, which indicate the water potentials at which g_i theoretically would fall to zero, were within 0.1 MPa. This indicates that, even though the maximum g_i and the sensitivity of the stomata may be determined by the environment or fertility, the water potential at $g_i = 0$ may be a characteristic of the specific cultivar. This particular point could bear further investigation.

The crop water stress index for 1987 illustrates that not only is it possible to generate a range of CWSI with the control system, but also that the correlations of CWSI with yield, mean SSD, and mean g_i are excellent (Fig. 9). Since all four of these parameters are related to stomatal function, these correlations are not unexpected. It should be noted that the CWSI curve predicts a somewhat higher maximum yield for 1987 (12.9 Mg ha⁻¹) than the SSD curve (11.1 Mg ha⁻¹). Whether this difference is statistically significant is unknown.

Table 2 shows the linear regression coefficients for relationships not included in the figures but which may be of interest to the reader.

Plants in all plots reached 50% pollen shed within 0.5 d of each other. Yield losses in 1987 can be attributed to reductions in numbers of kernels produced and/or weight per kernel, depending on the stress treatment (Table 3). The reduction in number of kernels per unit land area is associated with the number of days delay to 50% silking. A delay of 1.5 d seems not to matter; however, delays of 2 and 2.5 d resulted in kernel number reductions of 12 and 36%, respectively. The reason that a delay of 1.5 d to 50% silking was not important may be that 81% of the plants were silking on the day that pollen shed had reached 100% in this plot (Table 3), and >90% of the plants were silking on the following day. In the case of the cycle plot (2-d delay), the fraction of plants showing silk at

100% pollen shed was only 60% and did not rise to 100% for an additional 3 d. Comparable numbers for the sustained stress plot were 44% silking at 100% pollen shed, and the plants in this plot never reached 100% silking.

The cause of yield losses due to weight per kernel are somewhat more speculative. The cycle plot, in which the plants experienced the greatest stress during grain filling, also showed the greatest reduction in weight per kernel. The 15% reduction in weight per kernel that occurred in the early-stress plot may be associated with reduced growth during the vegetative period, which would have contributed to a lessened ability to fill the grain later. The fact that there was little or no reduction in weight per kernel in the sustained-stress plot, as might be expected on the basis of the stress during silking and early grain development (2,6), may be a result of the large decrease in number of kernels in this plot; thus, more photosynthate could have been available to the existing kernels even though the stress continued throughout grain filling.

CONCLUSIONS

We have demonstrated a method for the experimental control in the field of physiological parameters affected by water-deficit stress. Conceptually, the system is very simple, since the use of plant sensors relieves the investigator of the necessity for characterizing soil and atmospheric conditions to estimate crop water needs. The plants themselves integrate all the relevant environmental conditions, and the correct quantity of water may be applied to meet the plants' needs, or any given fraction thereof, through the judicious use of the appropriate water-application algorithms. Deficit irrigation can then become a practical experimental reality. Control of unwanted inputs of water to the system (precipitation) through the use of rain exclusion shelters should vastly improve the resolution of the system.

Although we used stomatal sensors for monitoring plant water needs and irrigation control, some other measure or indicator of water transport might work just as well and perhaps at much less cost and/or greater convenience. For instance, heat pulse measurements of sap velocity or stem flow could be used to provide a similar relative measure of the plants need for water. In addition, reasonable relationships between water stress and xylem acoustic emissions have been observed in the field (18), and there is no apparent reason why that technology could not be applied to the same end.

REFERENCES

- Bennett, J.M., J.M. Jones, B. Zur, and L.C. Hammond. 1986. Interactive effects of nitrogen and water stresses on water relations of field-grown corn leaves. *Agron. J.* 78:273-280.
- Claassen, M.M., and R.H. Shaw. 1970. Water deficit effects on corn: II. Grain components. *Agron. J.* 62:652-655.
- Fiscus, E.L. 1990. Field use of recording viscous flow porometers. p. 79-100. In Y. Hashimoto et al. (ed.) *Measurement techniques in plant science*. Academic Press, Orlando, FL.
- Fiscus, E.L., S.D. Wullschlegel, and H.R. Duke. 1984. Integrated stomatal opening as an indicator of water stress in *Zea*. *Crop Sci.* 24:245-249.
- Fiscus, E.L., S.D. Wullschlegel, and H.R. Duke. 1984. Stomatal sensors control the water supply to *Zea mays*. p. 278-285. In *Agricultural electronics: 1983 and beyond*. Vol. 1. ASAE, St. Joseph, MI.

6. Grant, R.F., B.S. Jackson, J.R. Kiniry, and G.F. Arkin. 1989. Water deficit timing effects on yield components in maize. *Agron. J.* 81:61-65.
7. Hunt, E.R., Jr., J.A. Weber, and D.M. Gates. 1985. Effects of nitrate application on *Amaranthus powellii* Wats: III. Optimal allocation of leaf nitrogen for photosynthesis and stomatal conductance. *Plant Physiol.* 79:619-624.
8. Idso, S.B., R.D. Jackson, P.J. Pinter, Jr., R.J. Reginato, and J.L. Hatfield. 1981. Normalizing the stress-degree-day parameter for environmental variability. *Agric. Meteorol.* 24:45-55.
9. Ishihara, K., H. Ebara, T. Hirasawa, and T. Ogura. 1978. The relationship between environmental factors and behavior of stomata in rice plants: VII. The relation between nitrogen content in leaf blades and stomatal aperture. *Jpn. J. Crop Sci.* 47:664-673.
10. Ishihara, K., O. Iida, T. Hirasawa, and T. Ogura. 1979. Relationship between nitrogen content in leaf blades and photosynthetic rate of rice plants with reference to stomatal aperture and conductance. *Jpn. J. Crop Sci.* 48:543-550.
11. Morgan, J.A. 1984. Interaction of water supply and nitrogen in wheat. *Plant Physiol.* 76:112-117.
12. Olesinski, A.A., S. Wolf, J. Rudich, and A. Marani. 1989. The effect of nitrogen fertilization and irrigation frequency on photosynthesis of potatoes (*Solanum tuberosum*). *Ann. Bot.* 64:651-657.
13. Oosterhuis D.M., and S. Walker. 1987. Stomatal resistance measurement as an indicator of water deficit stress in wheat and soybeans. *S. Afr. J. Plant Soil.* 4:113-120.
14. Radin, J.W. 1981. Water relations of cotton plants under nitrogen deficiency: IV. Leaf senescence during drought and its relation to stomatal closure. *Physiol. Plant.* 51:145-149.
15. Radin, J.W., and R.C. Ackerson. 1981. Water relations of cotton plants under nitrogen deficiency: III. Stomatal conductance, photosynthesis, and abscisic acid accumulation during drought. *Plant Physiol.* 67:115-119.
16. Radin, J.W., L.L. Parker, and G. Guinn. 1982. Water relations of cotton plants under nitrogen deficiency: V. Environmental control of abscisic acid accumulation and stomatal sensitivity to abscisic acid. *Plant Physiol.* 70:1066-1070.
17. Shanahan, J.R., and D.C. Nielsen. 1987. Influence of growth retardants, (anti-gibberellins) on corn vegetative growth, water use, and grain yield under different levels of water stress. *Agron. J.* 79:103-109.
18. Tyree, M.T., E.L. Fiscus, S.D. Wullschleger, and M.A. Dixon. 1986. Detection of xylem cavitation in corn under field conditions. *Plant Physiol.* 82:597-599.